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Observations on a Commensal Relationship of the Microhylid Frog *Chiasmocleis ventrimaculata* and the Burrowing Theraphosid Spider *Xenesthis immanis* in Southeastern Peru¹

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ABSTRACT

A commensal relationship of *Chiasmocleis ventrimaculata* and *Xenesthis immanis* was studied over a 3-mo period at Tambopata Reserved Zone, Peru. Observations indicate that both species simultaneously utilize the same diurnal retreats and forage in overlapping areas. Feeding trials suggest that *Xenesthis* readily feed on some species of anurans, and observations implicate the role of chemical defenses in preventing *Xenesthis* predation on *Chiasmocleis*. The commensalism is similar to that of ecologically similar terrestrial frogs and burrowing spiders in North America.

REPORTS OF ECOLOGICAL INTERACTIONS between spiders and frogs have documented predator-prey relationships and suggested that some spiders may be important predators of frogs, especially of juveniles (Neill 1948, Sharma & Sharma 1977, Groves & Groves 1978, Littlejohn & Wainner 1978, Formanowicz *et al.* 1981, Hayes 1983). However, some authors have shown that certain frogs are capable of avoiding spider predation. Szelistowski (1985) found that the Costa Rican poison-dart frog *Dendrobates pumilio* was unpalatable to the ctenid spider *Cupiennius coccineus*, which was shown to eat other frogs. Blair (1936) and Hunt (1980) describe an association in the southern United States in which the microhylid frog *Gastrophryne olivacea* inhabits active burrows of the theraphosid spider *Dugesia bentzi*. Powell *et al.* (1984) found the frog *Physalaemus pustulosus* in occupied burrows of the theraphosid spider *Aphonopelma* sp. in Mexico. We report here an association in southeastern Peru between the microhylid frog *Chiasmocleis ventrimaculata* (Andersson) and the burrow-dwelling theraphosid spider *Xenesthis immanis* (Ausserer).

METHODS

The study was done in 1986 on the Tambopata Reserve, a reserved zone consisting of 5500 forested hectares at 290 m, in the department of Madre de Dios, Peru. The

area receives approximately 3 m of rainfall per year, mostly between October and May (Erwin 1984).

X. immanis is a large theraphosid spider with a body length of 6 to 7 cm (theraphosids usually are referred to as "tarantulas," although true tarantulas are Old World members of the family Lycosidae). Burrows of *X. immanis* are relatively common beside forest trails at Tambopata; at one time, six occupied burrows occurred along 3.9 km of trail. The two burrows observed during this study were in primary forest, one beside a trail and one at the edge of a small, shaded, man-made clearing; the burrows were separated by approximately 0.5 km. The spiders remain hidden in the burrow for most of the day and emerge around dusk to take up positions around the entrance. *X. immanis* is a sit-and-wait or ambush predator that captures small animals that move through the area near the burrow.

C. ventrimaculata at Tambopata is a terrestrial, nocturnal frog with a snout-vent length of approximately 2 cm. Investigations concerning the taxonomic status of the Tambopata population are currently under way as part of a study of the entire herpetofauna of the site (R. McDiarmid & R. Cocroft, in prep.); there may be 3 or 4 distinct forms in western Amazonia currently under the name *ventrimaculata*. All adults observed at Tambopata Reserve were inhabiting active spider burrows. Like the spiders, these frogs remain underground during the day, emerge after dusk, and forage in the area around the burrow.

Observations were made between 4 May and 30 July 1986. A rheostat-controlled headlamp fitted with a red filter was mounted on a tripod 1.5 m from the burrow. Observations were made at the lowest light setting that

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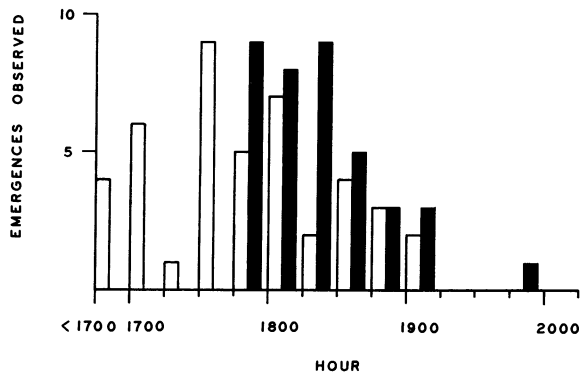


FIGURE 1. Timing of emergence of *Xenesthis immanis* (open bars) and *Chiasmocleis ventrimaculata* (solid bars) from Burrow A during the 3-mo study period.

allowed unambiguous observations, with one or two observers seated approximately 1.5 m from the burrow. Movements of each animal were recorded from the time it emerged from the burrow until it re-entered the burrow or until observations were ended. Most observations were made between 1630 and 1930, to include the time when the animals first emerged. Observations also were made between 1930 and 0700. The distance of an animal from the burrow was estimated to the nearest 1 cm for the first 10 cm and to the nearest 5 cm thereafter; directions with respect to the burrow were recorded using the 12-hr clock system. On 43 different days, 95 hr of observation were made at the two sites.

RESULTS

Most observations (83 hr) were made at the clearing burrow (Burrow A), both for ease of observation and because the number of burrow occupants was higher. The burrow was approximately 10 cm in diameter at ground level, narrowing to 6 to 7 cm in diameter below ground. Spiders in this burrow, an adult female (approximately 6.5 cm from front of cephalothorax to rear of abdomen) and 5 young (3.0–3.5 cm), usually emerged from 1700 to 1900 (Fig. 1); sundown was approximately 1730 during the study period. After emerging, spiders took up positions around the burrow perimeter and maintained a given location outside the burrow for 2 to 175 min ($\bar{x} = 30.9$), usually oriented away from the entrance (Fig. 2a). Spiders occasionally may have remained in one location for longer than observed; most observation periods were 2 to 3 hr. Individuals covered a relatively small area around the burrow, moving 2 to 30 cm ($\bar{x} = 6.3$) between locations. Disturbance by the observers or by small mammals moving past the burrow resulted in the spiders quickly moving toward or re-entering the burrow, usually re-emerging a few minutes later.

The adult female emerged on 28 out of 37 observation nights (76%); each time it emerged, it went to approximately the same position outside the burrow. The largest of the young spiders also returned to a relatively fixed position each night it emerged. The other young were not clearly distinguishable by size and may or may not have returned to the same positions on successive nights. Spiders usually were back in the burrow by daylight.

Four feeding attempts were observed at Burrow A during the 42 hr when spiders were above ground (not including feeding trials, discussed below). The adult female made two unsuccessful attempts on moths which flew over it less than 15 cm above the ground. A young spider on two occasions attempted to catch terrestrial beetles approximately 1 cm in length. One beetle was merely pressed into soft ground beneath the spider and not captured; the other was captured and eaten. On five other occasions spiders were observed to make similar darting motions, but the observers were unable to detect prey items and none of these attempts resulted in a capture.

The frogs at Burrow A usually emerged or appeared at the burrow entrance between 1745 and 1900, within 1.5 hr after sundown (Fig. 1). One to four frogs emerged ($\bar{x} = 1.96$), simultaneously or singly over a period of up to 65 min (Fig. 2b). Individuals were not marked, so this represents the minimum number of frogs utilizing the burrow during the study period. Often a frog remained in the entrance for up to 30 min before emerging. Once out of the entrance, the frogs adopted a modified sit-and-wait foraging mode, remaining in one location for 1 to 56 min ($\bar{x} = 14.0$) before moving to another location; locations were 2 to 40 cm apart ($\bar{x} = 12.3$). At least one frog emerged from the burrow on 25 out of 37 observation nights (68%). On 21 nights one to six spiders were above ground before the frogs emerged, and on 2 nights frogs and spiders emerged simultaneously. On one occasion five spiders and one frog were above ground at the start of observations. On only one night did frogs emerge while all spiders remained in the burrow; two frogs emerged and stayed within 2 cm of the entrance during the observation period. One re-entry was observed at this burrow, at 0425; in contrast to the cautious emerging behavior, the frog darted into the burrow from at least 50 cm away. This rapid motion may explain why re-entries were not detected during other early morning observations.

On eight different nights, 26 feeding attempts by frogs were observed, all within 5 cm of the burrow entrance. Distributing this number over the amount of time a frog was clearly visible and feeding observations were noted yields an individual rate of 2.6 feeding attempts per hour. This number is almost certainly an underestimate of the number of attempts made, as only when the observer could actually see a frog move forward and open its mouth was a motion counted as a feeding attempt. Motions made

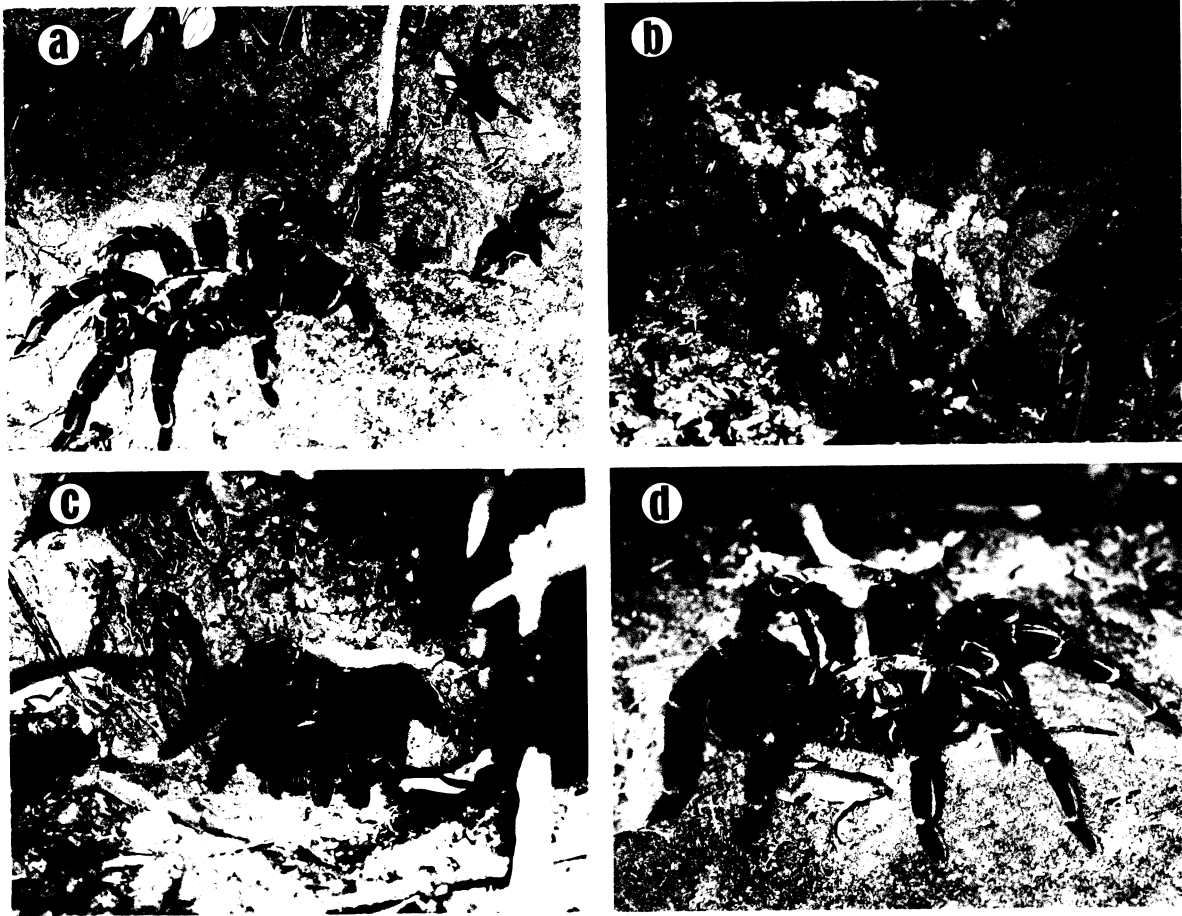


FIGURE 2. a. Adult female and three juvenile *Xenesthis immanis* in characteristic sit-and-wait positions outside Burrow A. Note emerging *Chiasmocleis ventrimaculata* and additional juvenile spider. b. Three individuals of *Chiasmocleis ventrimaculata* emerging simultaneously from Burrow A. c. A single individual of *Chiasmocleis ventrimaculata* emerging from Burrow B. d. An individual of *Chiasmocleis ventrimaculata* under the adult female *Xenesthis immanis* after emerging from Burrow A.

when the frog's foreparts were turned away from the observer or in shadow were not counted. Prey items, presumably too small to be observed from 1.5 m away, were not seen.

Burrow B, beside a trail, was inhabited by a single adult female spider and at least 2 frogs. This spider would approach the entrance of the burrow at dusk but rarely fully emerged. At least one frog emerged on four out of seven nights of observation. The frogs would emerge from 1720 to 1900 and move under the leaf litter near the burrow (Fig. 2c). In emerging, the frogs would push past or crawl under the spider, which frequently blocked the burrow entrance. No spider or frog feeding attempts were observed at this burrow.

A composite home range estimate was compiled for frogs and for spiders at Burrow A. An index of home

range area was calculated by the convex polygon technique (see Jennrich & Turner 1969), using the nightly maximum observed distance from the burrow for each individual (where available). *Xenesthis* individuals utilized an area of 0.21 m² during the study period ($N = 69$; Fig. 3). Although the range of *Chiasmocleis* broadly overlaps that of *Xenesthis*, the frogs ranged farther from and covered a greater area around the burrow, utilizing an area of 0.46 m² ($N = 37$; Fig. 4). The distances moved by the frogs represent a minimum. It was impossible to follow a single individual throughout an entire night, especially when one hid under vegetation; on occasion, frogs probably ranged farther than observed. The spiders, on the other hand, were always easily locatable when out of the burrow.

Xenesthis and *Chiasmocleis* showed some differential use of the area around the burrow. The opening of the

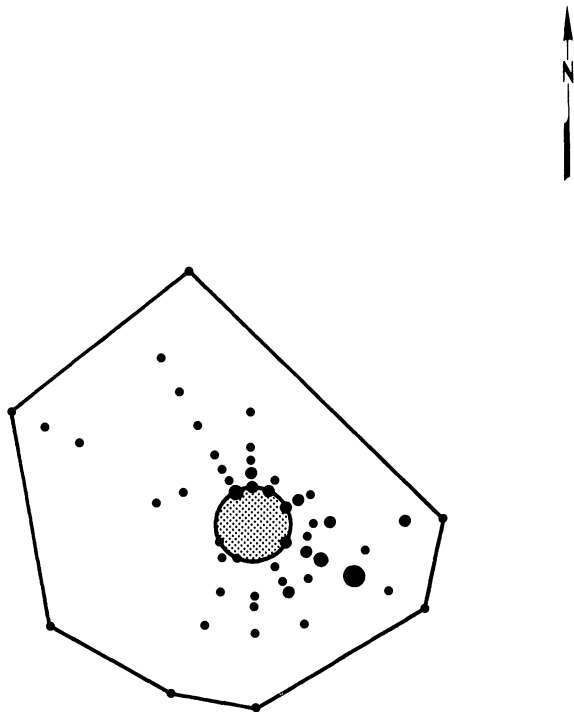


FIGURE 3. Composite range of individuals of *Xenesthis immanis* at Burrow A, assembled from maximum observed nightly distances from burrow ($N = 69$). The smallest dots represent a single point; the next larger, two points; the next larger, three points; the largest, five points. The burrow mouth (stippled area) has a diameter of 10 cm.

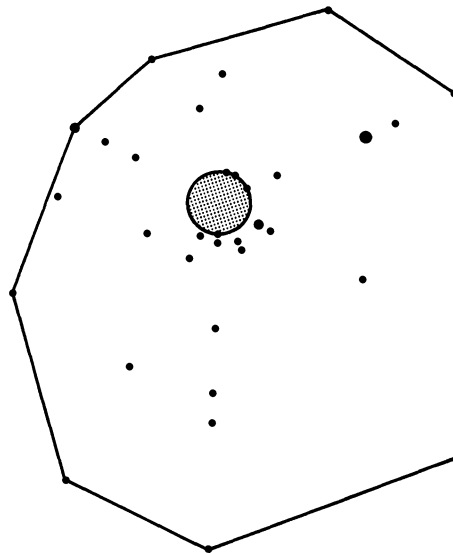


FIGURE 4. Composite range of individuals of *Chiasmocleis ventrimaculata* at Burrow A, assembled from maximum observed nightly distances from burrow ($N = 37$). The smallest dots represent a single point; the next larger, two points; the largest, three points. The burrow mouth (stippled area) has a diameter of 10 cm.

burrow was oriented eastward. The area south and east of the burrow was clear of vegetation; the area north and west of the burrow contained scattered herbaceous plants. Much of the spider activity was concentrated in the open area southeast of the burrow, whereas the frogs, once away from the burrow, showed some tendency to utilize more vegetated areas.

In 23 out of 50 emergences (46%) at Burrow A, frogs moved under a spider while or after emerging, crawling under the arch of the legs or under the body and often remaining there for an extended period (Fig. 2d). The spiders showed no response to the frogs' proximity except occasionally to shift a leg or raise the body off the ground when a frog moved underneath. Occasionally, a frog would move under a spider in response to observer movements or attempts to use brighter light.

On five occasions immature spiders pounced onto or towards a frog after it had emerged from the burrow; in each case, the spider remained motionless with its mouthparts poised over the frog, and, after a few seconds, one or the other moved away.

After five weeks of observations, pilot feeding trials were made in which frogs of six species (Table 1) were presented to the adult spider at Burrow A (the adult at Burrow B, which remained underground, was not used). This was done near the end of the study period to avoid altering the behavior of the spiders during base-line observations. After the spider accepted a frog, no further trials were made until the following day. Frogs were dropped or allowed to jump to within 50 cm of the adult spider. This spider readily captured and ate seven out of the nine frogs presented. Attack behavior apparently was triggered initially by the frog's movement and subsequently, on some occasions, by contact of the spider's leg or pedipalp with the frog after the spider moved over the area. With all but the smallest frogs, the adult carried the frog into the burrow, turned to face the entrance, and allowed one to two young to feed on the frog held in its chelicerae. Surveys of the area on the following day revealed no discarded parts, except, on one occasion, the partially eaten remains of a 6.1 cm *Bufo marinus* which lay 103 cm away from the burrow. The two frogs that were rejected (*Physa-*

laemus petersi) were pounced on by the adult (two trials each) and released unharmed after a few seconds; examination of the frogs showed that their skin was intact. This capture and release behavior was similar to that observed when immature spiders pounced on *C. ventrimaculata*. The behavior of the adult spider towards the introduced frogs, even those individuals of *P. petersi* that were released, was markedly different from its behavior towards the frogs living in the burrow; the cohabiting *C. ventrimaculata*, even when they jumped or crawled rapidly, evoked no predatory response.

To obtain an indication of the adult female spider's response to other vertebrates, especially potential frog predators that entered the burrow area, a 90-cm (total length) individual of the colubrid snake *Leptophis ahaetulla* was presented to the adult at Burrow A. The snake was anaesthetized and moved past the burrow on a monofilament line, about 50 cm from the adult female spider. The spider pounced on the snake, inserted its chelicerae into the snake's body 15 cm behind the head, and attempted to drag the snake into the burrow.

DISCUSSION

The pattern of interspecific interactions in this study is remarkably similar to the association of related, ecologically similar microhylid frogs and burrowing spiders in the southern United States reported by Blair (1936) and Hunt (1980). Like *C. ventrimaculata*, individuals of the frog *G. olivacea* are nonterritorial and several individuals may inhabit the same spider burrow, remaining underground during the day and foraging in the area around the burrow at night (Hunt 1980). Both spider species, *X. immanis* in Peru and *D. hentzi* in the United States, apparently use the burrows as retreat and nesting sites. Adult female spiders aggressively prevent other large organisms from entering the burrow. Hunt (1980) introduced garter snakes (*Thamnophis proximus*) into aquaria with burrows containing an adult female *D. hentzi* and several individuals of *G. olivacea*; the snakes preyed on frogs which were outside the burrow, but were repelled by the female spider and were unable to prey on frogs inside the burrow. In both associations, the frogs are tolerated in and around the burrow and on occasion take refuge under a spider in response to disturbance. The association of the leptodactylid frog *P. pustulosus* with the theraphosid *Aphonopelma* sp. in Mexico appears to be similar, in that more than one frog was tolerated within a single occupied spider burrow (Powell *et al.* 1984).

Why the spiders do not prey on the burrow-dwelling frogs is not clear. The small size of the frogs relative to the spiders does not seem to be a factor; in the Peru association, the adult *Chiasmocleis* were within the size range of frogs that were eaten. In the U.S., *Dugesia*

TABLE 1. Responses of adult female *Xenesthis immanis* to introduced frogs.

Frog species	Snout-vent length (cm)	Response of spider
Bufonidae		
<i>Bufo marinus</i>	4.1	Captured and ate
	6.1	Captured and ate
Hylidae		
<i>Hyla fasciata</i>	2.8	Captured and ate
<i>Phyllomedusa palliata</i>	4.6	Captured and ate
Leptodactylidae		
<i>Eleutherodactylus peruvianus</i>	~2.5	Captured and ate
<i>Leptodactylus wagneri</i>	1.5	Captured and ate
	1.7	Captured and ate
<i>Physalaemus petersi</i>	2.8	Captured and released
	~2.5	Captured and released

apparently are capable of preying on frogs and other small vertebrates (Gertsch 1979), and captive individuals will feed on crickets (Hunt 1980), which are similar in size to *G. olivacea*. *P. pustulosus*, approximately the same size as *P. petersi*, also appear to be suitably sized prey for *Aphonopelma*.

Many spiders are known to rely on chemical cues, substrate vibrations, or airborne pressure waves to locate and identify prey (Foelix 1982, Hergenröder & Barth 1983). *Xenesthis* and most other theraphosids are probably included in this group, since they have poor visual resolution (*e.g.*, Browning 1981) and are active primarily at night (Herrero & Valerio 1986, this study). Our observations and preliminary experimental data implicate the use of chemosensory cues in the recognition of *Chiasmocleis* by the burrowing spiders. Glandular skin secretions in frogs often contain compounds that render some species unpalatable or even toxic to potential predators (*e.g.*, Erspamer 1971, Myers & Daly 1976). Although no specific skin toxicity data are available for *Chiasmocleis*, the behavior of juvenile spiders in attacking and releasing the burrow-dwelling *Chiasmocleis* implicates the use of chemical cues in rejecting them as prey. The decision-making process apparently occurs while the frog is under the spider's chelicerae, which would place the frog outside the spider's field of vision, and the apparent lack of motion on the frog's part argues against the use of the vibrational cues. Chemosensory hairs in spiders are concentrated on the distal portions of the pedipalps (Foelix 1982), which appeared to be in contact with the frog's skin after the

spider had pounced on it. In addition, the capture and release behavior of the juvenile *Xenesthis* is similar to that of the ctenid spider *C. coccineus* when presented with poison-dart frogs (*D. pumilio*) (Szelistowski 1985), whose skin is known to be toxic.

Members of the *P. pustulosus* species group (including *P. petersi*, the sister species of *pustulosus*) all have very warty, pustular skin (Cannatella & Duellman 1984). Powell *et al.* (1984) suggest that noxious skin secretions protect *P. pustulosus* from being eaten by *Aphonopelma*. Since *P. pustulosus* is preyed upon by a range of vertebrate predators, including marine toads (Jaeger 1976), Philander opossums (Tuttle *et al.* 1981), and bats (Tuttle & Ryan 1981), its apparent immunity to predation by *Aphonopelma* raises the possibility of an anuran chemical defense having evolved, at least in part, in response to predation by invertebrates. The presence in small, terrestrial frogs of an antipredator defense against invertebrates would not be surprising, particularly in tropical forests, where spiders may be important predators of frogs (Formanowicz *et al.* 1981) and where the abundance of both frogs and spiders in the leaf litter (pers. obs.) would suggest that the potential for encounters is relatively high.

The three known associations of frogs and theraphosids do not appear to be obligate, and each involves an unknown proportion of the populations involved. In the south-central United States, *G. olivacea* occurs in spider burrows as well as a range of other microhabitats (Conant 1975). In Oklahoma, a large proportion of the *G. olivacea* population apparently takes refuge in *D. hentzi* burrows. Approximately 75 percent of over 100 *D. hentzi* burrows examined by Blair (1936) contained at least one *G. olivacea*, and during the driest weather this was apparently the only microhabitat where the frogs could be found. In Ecuador and eastern Peru, *Chiasmocleis* in the *ventrimaculata* complex have been collected in forest litter and low herbaceous growth away from spider burrows, and apparently breed in flooded areas in the forest (Duellman 1978, Schlüter 1984, R. W. McDiarmid and R. B. Croft, pers. obs.). The proportion of *X. immanis* burrows without frogs is not known. Relatively little information is available about the ecology of *P. pustulosus*, but it is clearly not restricted to spider burrows (see Ryan 1985 and references cited therein).

No benefits to burrowing spiders of allowing frogs to share the burrow are known, although Hunt (1980) suggested that ants are potential spider egg predators and that the ant-eating *G. olivacea*, by reducing the number of ants around the burrow, may reduce predation on spider eggs. For the frogs, however, a spider burrow, in the absence of spider predation, seems to provide a favorable microhabitat. By preventing potential frog predators such as snakes from entering the burrow, the adult spider provides a retreat from predation for burrow-dwelling frogs, and the proximity of discarded spider prey parts may result in a local concentration of invertebrate food items. Furthermore, Powell *et al.* (1984) suggest that inhabiting a spider burrow may reduce the risk of desiccation for a frog. Because one species benefits while the other apparently is unaffected, the relationship is probably best described as commensal.

Available evidence suggests that commensalism is a more important aspect of the biology of the burrow-dwelling frogs than of the spiders. Although occupying a spider burrow may not be necessary for survival, it seems to constitute an important and possibly advantageous microhabitat for some portion of the population. Further studies are planned to test the role of chemical cues in recognition of *Chiasmocleis*, *Physalaemus*, and other frogs by theraphosids. Also interesting would be an investigation of the possibility of similar associations in other parts of the Neotropics where burrowing theraphosids and small, terrestrial microhylids and leptodactylids occur.

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